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SPECIAL FEATURE: VEGETATION RESTORATION

Biomass accumulation during reed encroachment reduces efficiency of restoration of Baltic coastal grasslands

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Keywords
Boreal Baltic coastal meadows; Coastal salt marsh; Eutrophication; Grazing; Land-use change; Management; Nutrients; Restoration success

Abbreviations
DCA = Detrended Correspondence Analysis

Nomenclature
Kukk (1999)

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Abstract

Question: To what extent is restoration of vegetation in coastal grasslands delayed by accumulation of nutrients after abandonment of traditional management and subsequent reed encroachment? How does nutrient flow in the plant–soil system react to reintroduction of grazing?

Location: Coast of Baltic Sea, western Estonia.

Methods: Abandoned, continuously managed and restored coastal meadows were selected in four different study regions and their vegetation composition sampled. Nitrogen, P, K, Na, Ca and Mg concentrations and C/N ratios were determined in both vegetation and soil. Differences between management groups were evaluated.

Results: Comparison among different management groups revealed several differences in both relative and total amount of nutrients in soil and vegetation. Most soil properties of restored sites were similar to those in abandoned sites. Carbon stock in the soil profile doubled after abandonment, total N concentration in the top soil layer increased while plant available P concentration decreased. The phytomass and chemical composition of phytomass rapidly changed back to a 'normal' level after restoration. Species composition remained different, but species typical of coastal grasslands were present in restored sites. There was a strong site specificity in the results.

Conclusions: Re-establishment of grazing had a rapid impact on plant biomass of coastal grasslands. Species composition responded more slowly, but target species returned relatively quickly. Slow recovery of soil properties, however, means that the results of restoration may be fragile and return of tall-growth vegetation is very probable if managent intensity declines. Long restoration periods should be planned to reach pre-abandonment environmental conditions when using non-destructive restoration methods.

Introduction

Boreal Baltic coastal meadows (Natura 2000 code 1630*; they also belong to the Northern European group of maritime salt marshes, Chapman 1977) are considered of very high nature conservation value (Adam 1990; Allen & Pye 1992; Rannap et al. 2004), serving as a habitat for many rare and threatened amphibian, bird (especially waders) and plant species (Rebassoo 1975; Puurmann & Ratas 1998; Kuresoo & Mägi 2004). In the northern part of the Baltic Sea area, they are located in an area of post-glacial isostatic land uplift. During the last several thousands of years, in regions where the shores are flat, sea is shallow and wave action is small, the land that has risen from the sea has been immediately taken into use by man to pasture livestock. This has prevented accumulation of nutrients in the soil, has kept the soils of coastal grasslands young and developing, and has created habitats with short-stature vegetation. As in all other semi-natural meadows in the hemiboreal zone of Europe, the quality of coastal meadows for nature conservation directly depends on human-induced management, mostly grazing (Gibson et al. 1987;

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Jerling 1999; Jutila 2001; Burnside et al. 2007). However, the intensification of agriculture in the 20th century has made pasturing in coastal areas economically unprofitable and most coastal meadows have now been abandoned.

On abandoned Baltic coastal grasslands, *Phragmites australis* becomes dominant and forms dense and high reedbeds. During this process, species that are adapted to the low statue of the vegetation of grazed coastal meadows lose their habitat and a considerable drop in biodiversity is observed (Dijkema 1990; Esselink et al. 2000; Burnside et al. 2007; Wanner 2009). Recognition of species decline has initiated several restoration projects in coastal grasslands (e.g. Kokovkin 2005). However, removal of *Phragmites* stands can be rather expensive and labour intensive and is not always successful (Burdick & Dionne 1994; Marks et al. 1994; Chambers et al. 1999). Therefore, conservation agencies in the Baltic region usually do not employ destructive methods of reed removal (e.g. sod cutting) and in most cases rely only on reintroduction of grazing as a restoration tool and allow the ecosystem to develop without extensive man-made transformations. However, in such modest and low-input restoration events, return of favoured bird and plant species to areas where grazing is reintroduced often takes longer than expected (Kuresoo & Mägi 2004).

We hypothesize that restoration success on abandoned coastal grasslands is reduced by natural eutrophication that takes place during reed encroachment (see also Chambers 1997; Chambers et al. 1999; Bart & Hartman 2000). Reed is highly productive and in natural reedbeds most of the biomass remains ungrazed and enters the detritus system (Polunin 1984; Hocking 1989). In coastal areas, where decomposition and mineralization are reduced due to moist conditions, reedbeds not only accumulate a large amount of biomass and nutrients above ground, but also in soil. Mineralization of litter in reedbeds is also suppressed by the high C/N ratio (Polunin 1984) of shoots of *Phragmites*.

Reintroduction of grazing should quickly reduce the amount of plant biomass and change the flow of nutrients in restored sites. Changes in vegetation composition can also be expected to occur relatively fast if there is still a seed bank present in the soil (although after a long time of abandonment this is often not the case; see e.g. Thompson et al. 1997; Wolters & Bakker 2002; Wanner 2009) or when there is a nearby source for species immigration (e.g. Bernhardt & Koch 2003). But the inertia of soil development processes is strong and could prevent re-establishment of small plant species characteristic of coastal grasslands due to increased productivity, even if their immigration is not limited by availability of propagules (Onaindia et al. 2001; Van Dijk et al. 2007).

The aim of the current work is to estimate the extent to which restoration effects are delayed by changes in nutrient availability on abandoned coastal grasslands and how nutrient flow in the plant–soil system reacts to reintroduction of grazing. We approach the issue using comparative analysis of vegetation and soil properties of abandoned coastal meadows (reedbeds or reed-dominated sites), restored coastal meadows and well-preserved (grazed) coastal meadows. We address the following specific questions: (1) What happens to the soils after management of coastal grassland ceases? (2) How do soil and vegetation properties (especially their macronutrient concentrations) respond to reintroduction of grazing? (3) To what extent is restoration of vegetation in coastal grasslands delayed by presumed accumulation of nutrients after abandonment of traditional management and subsequent reed encroachment?

Methods

Fourteen different coastal grasslands in four regions were selected along the western coast of Estonia (Fig. 1) based on information on their management history. In each region, continuously managed, abandoned (neither grazed nor mown for at least 30 yr before the study) and restored (by means of re-establishment of grazing about 3–5 yr before the study) coastal grassland sites were selected as close to each other as possible in order to minimize the effect of site specificity on soils (e.g. effects of parent material, stoniness, texture, weather). Restored sites were selected as close to abandoned sites as possible (in Haeska and in Piirumi separated only by a fence between the pastures) in order to assure the similarity of the vegetation and management history prior to the start of restoration. Managed sites were selected as having as similar geomorphology to the abandoned sites as possible. There was no restored site available in northernmost Silma region. Managed sites had been grazed primarily with cattle and occasionally with sheep and horses at ca. 0.5–1.5 livestock units per hectare per year.

All studied grasslands were relatively large and wide, with a distance from the shoreline to the landward edge of the grassland mostly exceeding 500 m. A relatively homogeneous upper part of the saline zone (middle to upper geolittoral) was selected for the study in all sites, and special care was taken to select areas without a clearly detectable elevation gradient in order to minimize differences in salinity, effects of waves, sedimentation, etc., between plots, and to also ensure comparability between sites. Plant associations dominating in managed grasslands were *Elytrigietum repentis*, *Junco-Glaucetum* and *Festucetum rubrae*. Abandoned grasslands were almost completely dominated

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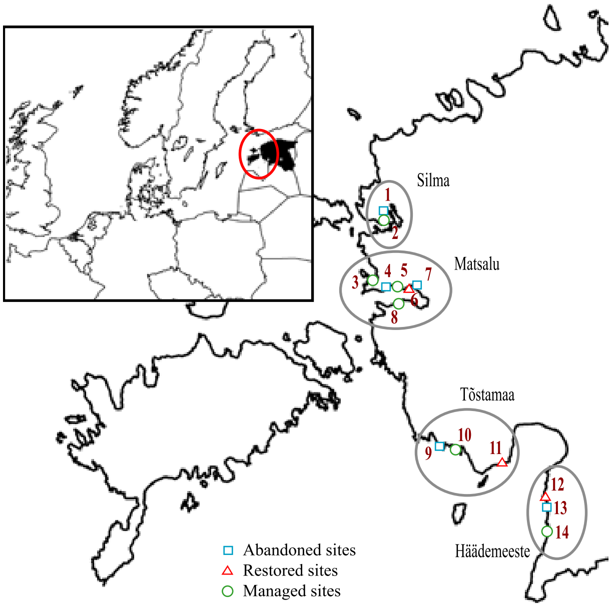

Fig. 1. Locations of the study sites in four regions on the western coast of Estonia. Site numbers: 1 – Pürksi (abandoned; 58°59′51″ N, 23°34′03″ E); 2 – Tahu (managed; 58°59′38″ N, 23°33′56″ E); 3 – Põgari (managed; 58°48′ 13″ N, 23°31′10″ E); 4 – Saardu (abandoned; 58°47′20″ N, 23°36′0″ E); 5 – Haeska I (managed; 58°46′52″ N, 23°39′24″ E); 6 – Haeska II (restored; 58° 46′58″ N, 23°41′44″ E); 7 – Haeska III (abandoned; 58°47′05″ N, 23°42′ 15″ E); 8 – Salmi (managed; 58°43′55″ N, 23°40′01″ E); 9 – Kastna (abandoned; 58°19′33″ N, 23°54′30″ E); 10 – Suti (managed; 58°18′55″ N, 23°58′30″ E); 11 – Kavaru (restored; 58°16′06″ N, 24°10′37″ E); 12 – Piirumi I (restored; 58°09′30″ N, 24°28′37″ E); 13 – Piirumi II (abandoned; 58°09′14″ N, 24°28′48″ E); 14 – Häädemeeste (managed; 58°5′27″ N; 24° 29′08″ E).

by *Phragmitetum australis* while restored sites did not have fully developed plant associations (transitional versions of *Deschampsio-Caricetum nigrae*, *Elytrigietum repentis* and *Phragmitetum* prevailed).

In each site 20 0.5 m × 0.5 m relevés were investigated on two 90-m long transects (ten plots per transect, 10-m apart) located 30 m from each other and perpendicular to the coastline. In each relevé, plant species composition was determined, cover of each species estimated and vegetation height measured. From each second relevé (ten plots per site) the central 10 cm × 50 cm part was sampled for measurement of plant standing biomass (litter was excluded), and from the rest of the plot at least 15 g of living plant material was collected for chemical analyses. In the central part of the same plots the depth of a humus layer (A, AT and AO horizons, hereinafter referred to as top layer) of soil was measured and soil samples from the top layer were collected for chemical analyses. One soil pit (up to 1-m deep) was excavated between the transects for description of soil type, generic soil layers and collecting samples for estimation of bulk density and C content of the soil. Plant biomass samples were dried at 80 °C for 48 h and then weighed. Samples for chemical analyses were air-dried. Field analyses were undertaken in Jul and Aug 2005.

Acid digestion with sulphuric acid solution was used to determine total content of P, K, Na, Ca and Mg in the plant material. After digestion, the content of total P was determined colorimetrically. Total K and Na content were determined by flame photometry and total Ca and total Mg were measured using atomic absorption spectroscopy. Total N and total C content of oven-dried samples were determined by the dry combustion method on a varioMAX CNS elemental analyser (ELEMENTAR, Germany).

Soil samples were air-dried, sieved through a 2-mm sieve and analysed for total N (Kjeldahl method), plant available P, K, Ca and Mg (Mehlich-3), organic C (Tjurin) and pH (KCl). Organic matter content of the soil was determined by weight loss after heating for 4 h at 500 °C. All chemical analyses were performed in the Laboratory of Soil Science and Agrochemistry of the Estonian University of Life Sciences. Carbon stock in the soil profile was calculated by multiplying bulk density of each soil layer with the depth and C content of that layer and then correcting for the area.

We employed two-way analysis of variance (ANOVA) to estimate differences between management groups, effect of region and regional differences in management effects (as estimated by the interaction between the factors 'region' and 'management'). All variables were tested for normal distribution of residuals of model predictions with the Shapiro test. Number of species and vegetation height were log-transformed and plant canopy cover was arcsin-transformed prior to analyses to obtain a fit with normal distribution. We employed Dunnett's modified Tukey-Kramer pair-wise multiple comparison test (DTK test) for detection of homogeneous groups.

Correlation between concentration of nutrients in the soil and in plants was tested using linear correlation analysis, which was performed separately for different management types as well as for the pooled data.

We used detrended correspondence analysis (DCA) in order to describe variation of vegetation composition and passively fitted environmental vectors on the resulting ordination. Linear correlation analysis was employed to estimate the relationship between the axes values for each site and the non-categorical environmental variables. Differences in diversity of vegetation between management groups were assessed with Shannon diversity and evenness indices.

Twenty-nine species commonly found in ecologically well-preserved coastal grasslands (pers. obs.) were selected to serve as indicator or target species for evaluation of

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restoration success (Appendix S1; hereinafter 'typical coastal grassland species'). Species selection was guided by the database of habitat preferences of Estonian species (Sammul et al. 2008). Relative frequency of presence in relevés (occurrence probability) of these species was calculated per each management group and arcsin-transformed to obtain normal distribution. Mean occurrence probabilities were compared between management groups with paired *t*-tests assuming unequal variance and with Welch adjustment to the degrees of freedom.

All statistical analyses were carried out with the R software version 2.10.1 (R Development Core Team, Vienna, Austria). DCA was carried out using the package VEGAN (version 1.17-0), and environmental vectors were fitted using the function 'envfit' with 999 permutations.

Results

Vegetation properties

Management had a strong influence on most vegetation properties (Table 1). Abandoned sites had larger plant canopy cover, taller vegetation and more plant biomass than managed and restored sites. Managed and restored sites had more diverse vegetation (more species per relevé, increase in diversity indices). Concentrations of N and Na were larger in plants of managed and restored sites than in plants of abandoned sites. Only the concentration of P and Ca, as well as the C/P and N/P ratios, in plants did not differ between sites with different management. Most of the vegetation properties in restored sites were similar to those of managed sites, while abandoned grasslands formed a separate homogeneous group. The exceptions to the above were mean Shannon diversity index and evenness of vegetation (restored sites were a separate homogeneous group with intermediate diversity values between low-diversity abandoned sites and high-diversity managed sites), concentration of Mg in plants (restored sites and abandoned sites were similar and both differed from managed sites), concentration of K in plants (plants in restored sites had a lower concentration of K than plants in managed or abandoned sites) and C/N ratio (managed sites did not differ from either restored or abandoned sites while the latter differed from each other).

There was also a strong difference between different regions in most vegetation properties. Only concentration of Mg, C/P ratio and N/P ratio in plants did not differ between different regions. Regional differences were also pronounced in the significance of the interaction between the effects of management and region, however, most interactions were ordinal and only N concentration in plants had a disordinal interaction between region and management.

Soil properties

The soils of the coastal grasslands studied are classified as Gleyic Fluvisols (Sodic), Histic Fluvisols (Sodic) and Eutric Histosols (Endofluvic features; WRB 2006). Soils have developed on sand or clay as parent material, they are moist and with slightly developed profiles. Abandoned areas with a fully developed reedbed had a very thick and tough top layer of soil with large quantities of roots and litter of *Phragmites*. Five of the grasslands had turf layers deeper than 10 cm. Two of these grasslands belong to group of abandoned grasslands (Pürksi: total range of turf layer 7–16 cm, share of plots with turf layer over 10 cm deep 60%; Kastna: 10–46 cm, 70%), two sites were managed (Häädemeeste: 8–23 cm, 80%; Suti: 10–19 cm; 90%) and one site was restored (Piirumi restored: 5 –25 cm, 30%).

Management has a statistically significant influence on all soil properties studied except for C stock in the soil profile (Table 2). There was a two-fold difference in C soil stock between managed sites and either abandoned or restored sites; however, due to large variations and lack of replication (only one value could be estimated per each site) this difference is not statistically valid. Most soil parameters did not differ between restored and abandoned sites, whereas managed sites formed a separate homogeneous group. The exceptions were the depth of the top layer, N content and P content, for which managed and abandoned sites form separate homogeneous groups, while restored sites did not differ from sites of other types due to a large variation. Soils of managed sites had a shallower top layer, smaller organic matter content, smaller N, C and Mg concentration and C/N ratio, but higher P and Ca concentration, as well as higher pH, than abandoned sites.

The regional differences were important for the depth of top layer, pH and concentrations of K, Ca, Mg and C/N ratio of soils. The interaction of management and region was significant for all estimated soil parameters except P content in soils. Most interactions were ordinal, but K and Ca content in soil were disordinal.

The content of a particular mineral element in the soil was only infrequently correlated with its content in the plants (Table 3) and correlations were rare in several management types simultaneously. Content of P in plants was negatively correlated with its content in soil in restored sites, content of Mg in plants was negatively correlated with its content in soil in abandoned sites and when the data from different management groups were pooled. Content of Ca in plants was negatively correlated with Ca content in soil in managed sites and in pooled data. There was a positive correlation between C/N ratio in plants and in soil in managed sites and a negative correlation between C/N ratio in plants and soil in restored sites.

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Table 1. Mean values (with 95% confidence intervals) and homogeneous groups (a, b, or c; at $P < 0.05$) of vegetation characteristics and chemical properties of plant biomass from different management groups, with the results of two-way ANOVA for differences between management groups (df $F_{(effect,\ error)}$ of traits from no. species through evenness = 2, 269; for chemical properties df = 2, 129), between regions (df = 2, 269 and df = 2, 129, respectively) and their interaction (df = 5, 269 and df = 5, 129).

Dependent variable	Mean values and homogeneous groups							*F*-Value of a comparison		
	Management Group			Region						
	Managed N = 100^{i}; 50^{ii}; 20^{iii}	Restored N = 120; 60; 24	Abandoned N = 60;30;12	Häädemeeste N = 60; 30; 12	Matsalu N = 120; 60; 24	Silma N = 40; 20; 8	Tõstamaa N = 60; 30; 12	Between management groups	Between regions	Interaction management * region
Number of species (0.25 m^{-2})^{i}	10.2 ± 0.8^{a}	9.27 ± 0.88^{a}	7.78 ± 0.75^{b}	11.6 ± 1.3^{c}	9.44 ± 0.71^{b}	$8.03 \pm 0.71^{a,b}$	6.72 ± 0.80^{a}	F = 16.8***	F = 22***	F = 16.5***
Plant canopy cover (%)^{i}	63 ± 3^{a}	57 ± 4^{a}	71 ± 4^{b}	72 ± 4.3^{c}	61.7 ± 3.1^{b}	54.8 ± 5.8^{a}	68.9 ± 4.8^{c}	F = 19.9***	F = 18.8***	F = 4.32**
Vegetation height (cm)^{i}	15.8 ± 1.5^{a}	18.7 ± 2.5^{a}	106 ± 17^{b}	36 ± 11^{a}	36.3 ± 8.3^{a}	44.2 ± 9.3^{a}	88.8 ± 28^{b}	F = 242***	F = 15.7***	F = 15.4***
Plant above-ground biomass (g m^{-2})^{ii}	305 ± 36^{a}	292 ± 71^{a}	652 ± 126^{b}	$21.3 \pm 4.2^{a,b}$	18.1 ± 2.8^{a}	17.9 ± 5.7^{a}	30.1 ± 10^{b}	F = 28***	F = 7.60***	F = 5.29***
Shannon diversity index^{i}	1.77 ± 0.07^{a}	1.56 ± 0.11^{b}	1.35 ± 0.12^{c}	1.75 ± 0.14^{a}	1.65 ± 0.08^{a}	1.54 ± 0.13^{a}	1.26 ± 0.14^{b}	F = 24***	F = 5.44**	F = 7.67***
Evenness^{i}	0.79 ± 0.01^{a}	0.72 ± 0.03^{b}	0.66 ± 0.04^{c}	0.74 ± 0.03^{a}	0.76 ± 0.02^{a}	0.75 ± 0.05^{a}	0.66 ± 0.06^{b}	F = 28***	F = 28***	F = 28***
N (%)^{ii}	1.68 ± 0.12^{a}	1.73 ± 0.21^{a}	1.47 ± 0.11^{b}	1.88 ± 0.23^{b}	1.51 ± 0.12^{a}	1.36 ± 0.07^{a}	1.73 ± 0.09^{b}	F = 8.58***	F = 13.8***	F = 28.8***, d
P (%)^{ii}	0.054 ± 0.008^{a}	0.046 ± 0.011^{a}	0.05 ± 0.01^{a}	0.06 ± 0.01^{b}	0.046 ± 0.007^{a}	0.04 ± 0.004^{a}	$0.05 \pm 0.009^{a,b}$	$F = 1.59^{n.s.}$	F = 4.84**	F = 13.64***
K (%)^{ii}	1.55 ± 0.10^{a}	1.19 ± 0.09^{b}	1.53 ± 0.15^{a}	$1.48 \pm 0.19^{b,\ c}$	$1.41 \pm 0.11^{a,b}$	1.25 ± 0.07^{a}	1.69 ± 0.15^{c}	F = 9.41***	F = 10.1***	F = 3.08*
C (%)^{iii}	42.5 ± 1.1^{a}	41.5 ± 0.9^{a}	42.3 ± 1.1^{a}	41.7 ± 1.1^{a}	42.2 ± 0.9^{a}	43.8 ± 1.9^{a}	41.7 ± 1.4^{a}	$F = 0.92^{n.s.}$	$F = 1.43^{n.s.}$	F = 2.66*
Na (%)^{ii}	1.32 ± 0.24^{a}	0.98 ± 0.26^{a}	0.40 ± 0.15^{b}	0.45 ± 0.11^{a}	1.20 ± 0.27^{b}	$0.73 \pm 0.27^{a,b}$	0.94 ± 0.27^{b}	F = 23***	F = 6.71***	$F = 1.89^{n.s.}$
Ca (%)^{ii}	0.30 ± 0.05^{a}	0.25 ± 0.04^{a}	0.25 ± 0.02^{a}	0.19 ± 0.03^{a}	0.28 ± 0.04^{b}	0.38 ± 0.07^{c}	0.27 ± 0.03^{b}	$F = 2.62^{n.s.}$	F = 11.0***	F = 9.72***
Mg (%)^{ii}	0.46 ± 0.03^{a}	0.36 ± 0.03^{b}	0.36 ± 0.03^{b}	0.41 ± 0.04^{a}	0.43 ± 0.03^{a}	0.39 ± 0.05^{a}	0.37 ± 0.04^{a}	F = 14.6***	$F = 1.50^{n.s.}$	F = 2.43*
C/N ratio^{iii}	$27 \pm 3^{a,b}$	25 ± 4^{b}	31 ± 1^{a}	24.4 ± 4.9^{a}	30.5 ± 3.6^{b}	$30.6 \pm 2.0^{a,b}$	25.0 ± 2.6^{a}	F = 4.81*	F = 4.47**	F = 9.10***
C/P ratio^{iii}	1333 ± 501^{a}	1844 ± 958^{a}	1157 ± 364^{a}	1599 ± 899^{a}	1471 ± 542^{a}	1158 ± 193^{a}	1125 ± 590^{a}	$F = 1.52^{n.s.}$	$F = 0.53^{n.s.}$	F = 4.29**
N/P ratio^{iii}	46 ± 14^{a}	67 ± 31^{a}	44 ± 19^{a}	59 ± 27^{a}	49.7 ± 18.6^{a}	37.8 ± 5.8^{a}	47.9 ± 28^{a}	$F = 1.52^{n.s.}$	$F = 0.26^{n.s.}$	F = 3.23*

[i]Variables for which sample size is given as the first figure after N.

[ii]Variables for which sample size is given as the second figure after N.

[iii]Variables for which sample size is given as the third figure after N.

N = samples size; $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; $^{n.s.}$not significant; d = disordinal interaction.

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Table 2. Mean values (with 95% confidence intervals) and homogeneous groups (a, b, or c; at $P < 0.05$) of soil properties for different management groups with results of two-way ANOVA for differences between management groups (df of $F_{(\text{effect, error})} = 2, 129$), between regions ($df = 2, 129$) and their interaction ($df = 5, 129$).

Dependent variable	Mean values and homogeneous groups							*F*-Value of a comparison		
	Management group			Region						
	Managed N = 50†; 5‡	Restored N = 60†; 6‡	Abandoned N = 30†; 3‡	Häädemeeste N = 30†; 3‡	Matsalu N = 60†; 6‡	Silma N = 20†; 2‡	Tõstamaa N = 30†; 3‡	Between management groups	Between regions	Interaction management* region
Depth of top layer (cm)	10.0 ± 1.2^{a}	$11.6 \pm 2.0^{a,b}$	13.1 ± 2.5^{b}	13.9 ± 2.13^{b}	7.63 ± 0.65^{a}	9.45 ± 1.24^{a}	18.1 ± 3.40^{c}	$F = 4.95^{**}$	$F = 30^{***}$	$F = 3.19^{**}$
Organic matter content (%)	35 ± 4^{a}	42 ± 6^{b}	47 ± 5^{b}	40.1 ± 6.74^{a}	40.0 ± 4.55^{a}	42.3 ± 4.24^{a}	41.9 ± 6.72^{a}	$F = 10.5^{***}$	$F = 0.17^{\text{n.s.}}$	$F = 10.9^{***}$
Bulk density of top layer (g cm^{-3})	0.42 ± 0.11^{a}	0.26 ± 0.15^{a}	0.23 ± 0.12^{a}	0.26 ± 0.16	0.36 ± 0.16	0.24 ± 0.20	0.36 ± 0.10	$F = 2.92^{\text{n.s.}}$	Could not be estimated	Could not be estimated
PH$_{KCl}$	6.10 ± 0.2^{a}	5.57 ± 0.2^{b}	5.68 ± 0.20^{b}	5.70 ± 0.30^{b}	$5.99 \pm 0.21^{b,c}$	5.26 ± 0.19^{a}	6.04 ± 0.16^{c}	$F = 21^{***}$	$F = 22^{***}$	$F = 44^{***}$
N (%)	1.26 ± 0.14^{a}	$1.52 \pm 0.22^{a,b}$	1.52 ± 0.16^{b}	1.60 ± 0.23^{a}	1.30 ± 0.15^{a}	1.45 ± 0.13^{a}	1.41 ± 0.23^{a}	$F = 4.32^{*}$	$F = 1.79^{\text{n.s.}}$	$F = 8.23^{***}$
C (%)	11.4 ± 1.4^{a}	17.0 ± 2.9^{b}	17.0 ± 2.4^{b}	13.1 ± 2.45^{a}	14.9 ± 2.21^{a}	14.7 ± 1.48^{a}	15.4 ± 3.17^{a}	$F = 15.3^{***}$	$F = 1.55^{\text{n.s.}}$	$F = 15.2^{***}$
P (mg·kg^{-1})	32 ± 8^{a}	$34 \pm 20^{a,b}$	21 ± 5^{b}	63.1 ± 19.2^{b}	24.0 ± 6.1^{a}	15.0 ± 5.5^{a}	12.0 ± 4.93^{a}	$F = 3.88^{*}$	$F = 26^{\text{n.s.}}$	$F = 13.7^{\text{n.s.}}$
K (mg·kg^{-1})	441 ± 60^{a}	341 ± 66^{b}	$414 \pm 59^{a,b}$	292 ± 75^{a}	461 ± 61^{b}	452 ± 44^{b}	$397 \pm 76^{a,b}$	$F = 3.22^{*}$	$F = 5.36^{**}$	$F = 13.6^{***}$, d
Ca (mg·kg^{-1})	2009 ± 532^{a}	928 ± 105^{b}	1025 ± 201^{b}	961 ± 302^{a}	2070 ± 519^{b}	599 ± 77^{a}	1153 ± 188^{a}	$F = 12.3^{***}$	$F = 9.41^{***}$	$F = 7.98^{***}$, d
Mg (mg·kg^{-1})	1147 ± 165^{a}	1671 ± 177^{b}	1729 ± 173^{b}	1347 ± 202^{a}	1319 ± 193^{a}	$1534 \pm 102^{a,b}$	1837 ± 226^{b}	$F = 22.7^{***}$	$F = 6.83^{***}$	$F = 13.2^{***}$
C/N ratio	9.0 ± 1.4^{a}	11.3 ± 2.9^{b}	11.7 ± 2.4^{b}	8.03 ± 0.78^{a}	11.1 ± 0.84^{b}	$10.1 \pm 0.61^{a,b}$	11.8 ± 2.96^{b}	$F = 7.83^{***}$	$F = 6.87^{***}$	$F = 10.2^{***}$
C stock in soil profile (t·ha^{-1})	64 ± 15^{a}	122 ± 58^{b}	122 ± 120^{b}	81 ± 27	80 ± 41	50 ± 40	179 ± 194	$F = 0.7^{\text{n.s.}}$	Could not be estimated	Could not be estimated

†Applies to all dependent variables except bulk density and C stock in soil profile.
‡Applies to bulk density and C stock in soil profile.
N = samples size;
$^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; $^{\text{n.s.}}$not significant; d = disordinal interaction.

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Table 3. Linear correlations between estimated chemical properties of soils and plants. Statistically significant correlations are printed in bold.

Correlation (Plants vs soil)	Managed		Restored		Abandoned		Pooled	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*
N	0.018	0.89	−0.29	0.12	−0.0005	0.99	−0.09	0.29
P	0.18	0.17	**−0.39**	**0.031**	0.27	0.055	−0.026	0.76
K	−0.10	0.43	−0.36	0.050	0.096	0.51	0.014	0.87
Mg	0.002	0.99	0.33	0.071	**−0.41**	**0.003**	**−0.27**	**0.001**
Ca	**−0.44**	**0.0004**	−0.008	0.97	−0.050	0.73	**−0.30**	**0.0003**
C	**0.30**	**0.0007**	−0.018	0.89	0.009	0.93	0.059	0.33
C/N ratio	**0.53**	**<0.0001**	**−0.57**	**<0.0001**	−0.17	0.097	0.0003	0.99

r = Pearson correlation coefficient; *P* = probability level.

Species composition

The DCA on the species abundances produced four axes with eigenvalues of 0.76, 0.62, 0.43 and 0.32. The managed habitats and the restored habitats formed distinct groups in an ordination plane (Fig. 2), suggesting different vegetation composition. However, the abandoned habitats were very scattered, showing very large variations in vegetation composition of abandoned sites. The correlation of DCA axes with environmental parameters is given in Table 4. Axis 1 is primarily related to vegetation characteristics. The variation is led by the effect of management – abandoned sites are located on the positive side and managed sites on the negative side of DCA axis 1 (Fig. 2a). The axis is also negatively correlated with soil pH and positively correlated with vegetation height, which is effectively determined by management regime. DCA axis 2 is positively correlated with parameters indicating low mineralization rate and accumulation of biomass in soil (soil C content, organic matter content and C/N ratio, but also Mg content). The negative end of DCA axis 2 primarily indicates high species richness of a habitat.

The distribution of species in an ordination plane revealed a distinction between different ecological groups (Fig. 2b). The positive end of DCA axis 1 is characterized by tall species of productive habitats (e.g. *Urtica dioica* and *Anthriscus sylvestris*), while at the negative end typical coastal grassland species aggregate (e.g. *Plantago maritima,*

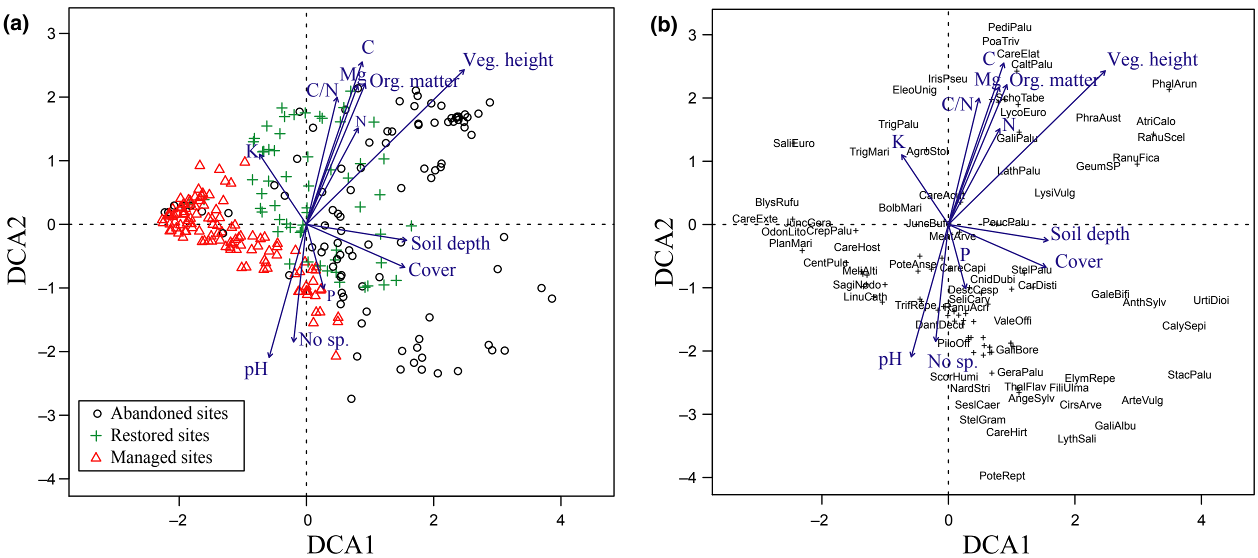

Fig. 2. Distribution of individual relevés (**a**), all 280 relevés included, and species (**b**) in the ordination diagram for the first two axes of the DCA. Environmental vectors are neutrally fitted into the ordination plane if their correlation with DCA axes is statistically significant at $P < 0.05$ (see also Table 4). In (**b**), where species names overlap, higher priority for plotting the name is given to the more abundant species: less abundant species are plotted as crosses (+). Abbreviations of environmental variables: pH – soil pH; No Sp – number of vascular plant species in relevé; Cover – plant canopy cover; Soil Depth – depth of the top layer of soil; Veg. Height – vegetation height; Org. Matter – organic matter content of soil; N – nitrogen content in soil; C – carbon content in soil; Mg – magnesium content in soil; C/N – C/N ratio in soil; K – potassium content in soil; P – phosphorus content in soil. Species names are given in Appendix S1.

Table 4. Linear correlations between between site scores on DCA axes and non-categorical environmental variables.

Variable	DCA1	DCA2	DCA3	DCA4
Number of species	−0.36***	−0.35***	0.19**	0.18**
Plant canopy cover	0.17**	0.19**	0.29**	0.10n.s.
Vegetation height	0.52***	0.36***	0.15*	−0.13*
Depth of top layer	0.32***	−0.12*	0.10n.s.	−0.12*
Organic matter content in soil	0.47***	0.47***	0.07n.s.	−0.10n.s.
pH of soil	−0.41***	−0.22***	−0.15*	0.30***
N content in soil	0.32***	0.31***	0.06n.s.	−0.04n.s.
C content in soil	0.49***	0.54***	0.06n.s.	−0.24***
C/N ratio in soil	0.33***	0.38***	−0.04n.s.	−0.14*
P content in soil	−0.06n.s.	−0.15*	0.19**	0.04n.s.
K content in soil	0.20***	0.23***	0.02n.s.	0.22***
Ca content in soil	−0.07n.s.	0.02n.s.	0.13*	−0.10n.s.
Mg content in soil	0.46***	0.43***	−0.01n.s.	0.01n.s.

r = Pearson correlation coefficient; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s. not significant.

Odontites spp., *Juncus gerardii*, *Carex extensa* and *Blysmus rufus*). The positive end of DCA axis 2 is characterized by species of moist habitats (e.g. *Pedicularis palustris*, *Carex elata*, *Eleocharis uniglumis*, *Iris pseudacorus* and *Caltha palustris*). The negative end of DCA axis 2 is characterized by species of alkaline and species-rich habitats (e.g. *Sesleria caerulea*, *Scorzonera humilis*, *Nardus stricta* and *Pilosella officinarum*).

Mean relative occurrence frequency of typical coastal grassland species was highest in relevés of managed meadows and lowest in abandoned meadows (Fig. 3). The difference was statistically significant at $P < 0.006$ (two-tailed test, $df = 28$, $t = 3.02$). Selected species were less common in restored sites, but this difference did not differ from that of managed sites ($t_{(28)} = 1.34$, $P = 0.19$), while being different from that of abandoned sites ($t_{(28)} = 2.39$, $P < 0.024$).

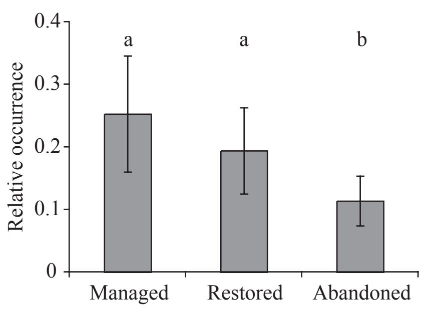

Fig. 3. Relative occurrence of typical coastal grassland species in relevés of the three studied management groups. Distribution of 29 species was analysed, bars denote 95% confidence intervals of the mean, and statistical differences between mean values are denoted with different letters.

Discussion

Grazing has been a traditional and regularly induced disturbance in Boreal Baltic coastal grasslands to which local species have adapted and which sustains local biodiversity, primarily by maintaining low-stature vegetation (Puurmann & Ratas 1998; Burnside et al. 2007; Wanner 2009). Depending on the differences between regions (e.g. abundance of reed or other habitats in a region), increasing height of vegetation or even a change from low-stature vegetation to a reedbed may or may not be considered favourable for nature conservation (see also Bakker et al. 1997). Such effects are especially debatable for bird species (Koivula & Rönkä 1998; Milsom et al. 2000; Bakker et al. 2003; Ottvall & Smith 2005). In the northern Baltic Sea area, following coastal grassland abandonment, bird diversity (especially waders) in most cases starts an immediate decline (e.g. Helle et al. 1988; Kuresoo & Mägi 2004). Plant diversity, however, often initially increases (e.g. Jutila 1997), only to decline in later stages of succession, especially after tall and dense reedbeds start to develop (see also Vestergaard 1998). After establishment of reed, distribution of typical small-stature seashore plants is restricted to the edges or occasional short-term openings within the reedbeds (pers. obs.). Our results indicate that in such abandoned sites with tall and *Phragmites*-dominated vegetation the different productivity components do not change in a uniform manner. Comparing abandoned sites to managed sites, N content in soil increases while P content decreases, even though the latter effect is not uniform across the regions studied. Nitrogen is typically the predominant limiting nutrient for salt marsh plants (Mendelssohn & Morris 2000; but see Van Wijnen & Bakker 1999 for more detailed analysis), in common with wetland plants in general (Van Duren & Pegtel 2000; Van de Riet et al. 2010), thus its increase could be interpreted as increased productivity. However, considering the large amount of organic C in soils of abandoned sites, one could assume that a large amount of N is actually bound with organic compounds in soil thus making it unavailable for plant growth. Carbon addition has even been used as a means to create N deficiency and reduce plant growth (Eschen et al. 2006; Reynolds & Haubensak 2009 and references therein). In our abandoned sites, the C/N ratio is higher than in managed sites, indicating a possible reduction in relative N availability. Moreover, in abandoned sites the availability of P is very low, making it the primary limiting factor for plant growth (see also Olff et al. 1997; Van Wijnen & Bakker 1997). Thus, the availability of nutrients in soil does not clearly increase with abandonment, as was initially hypothesized; yet plant biomass production increases considerably.

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The increase in plant biomass is due to the increased abundance of tall and competitive species with high relative growth rates – most notably *Phragmites australis*. *Phragmites* has a broad ecological amplitude and grows best in nutrient-rich habitats (Hocking et al. 1983; Güsewell & Koerselman 2002). It is also a species in which growth clearly benefits from increased N levels but is not as sensitive to variation in P levels (Romero et al. 1999). Eutrophication of the Baltic Sea (Rönnberg & Bonsdorff 2004) has probably contributed to the increased spread of *Phragmites*. Moreover, it has been shown that the disturbances from accumulation of wrack, to which large amounts of litter of *Phragmites* contribute, benefits its growth in some parts of coastal salt marshes (Minchinton 2002). Thus, there are several factors that simultaneously facilitate and even create a positive feedback for the development of reedbeds in abandoned coastal meadows.

The increased amounts of nutrients in soils of abandoned sites did not result in increased concentrations of mineral elements in plant biomass (Tables 1, 3). This suggests that mineralization of nutrients and their flow in the plant–soil system is reduced in such sites. The difference is again attributable to the dominance of tall grasses, mostly *Phragmites*. Importantly, low availability of N (in particular) and excess of C in plant litter decreases the speed of decomposition of litter and mineralization. This also affects mineralization of P, creating a strong deficiency of plant available P in soil and reducing P content in plants to extremely low levels. Considerable increases in the amounts of litter and poorer conditions for its decomposition lead to a large accumulation of organic matter in soils of abandoned sites, perhaps best illustrated as a two-fold increase in C stock in the soil profile. This change actually alters the whole structure of the soils – while soils of managed grasslands mostly belong to the class of mineral soils, soils of abandoned sites should mostly be classified as Histic Fluvisols and thereafter to Histosols (WRB 2006). This means that these soils have a considerable turf layer, reduced pH and provide completely different growth conditions for plants, as well as soil biota (e.g. Butt & Lowe 2004; Ivask et al. 2009). It is possible that reedbeds develop faster on sites where a turf layer is already present, in which case our results present not so much an effect of abandonment but rather regional differences in geomorphology of the coast, effect of elevation, etc. However, as we paid special attention to avoiding such effects when selecting the study sites, and also considering the number of sites and regions studied, we are certain that this is not the case. So far evidence of the impact of grazing on accumulation of biomass in soils is contradictory. Jeschke (1983) describes how on the German coast of the Baltic Sea trampling and soil compaction in grazed areas leads to reduced levels of decomposition and a build-up of organic matter (see also Cuttle 2008). Vestergaard (1998), on the other hand, describes accumulation of organic matter due to grassland abandonment on the southern Baltic coasts in SE Denmark, supporting our conclusions. Both studies also report the loss of a typical coastal grassland due to reed encroachment. There could be regional differences that are important to consider. While in the southern Baltic, the brackish coastal meadows are naturally on peaty soils, in the northern Baltic such accumulation of peat is considered an aberrance from the 'natural' state of coastal grasslands and, as such, a conservationally unfavourable process (see also Dijkema 1984) despite possible enhanced C sequestration (Chmura et al. 2003). Moreover, as our results also demonstrate differences between study areas, local conditions (such as differences in bedrock and geomorphology of the coast) could strongly affect the dynamics of coastal ecosystems. However, there could also be a discrepancy between the exact processes discussed. In the first case, the effect of trampling is discussed in areas that are still grasslands, and where soil compaction is an important factor. In the second case, the whole community (or even an ecosystem) is changing from grassland to reedbed and the importance of trampling is downgraded by the effect of increased production of plant biomass and increased litterfall.

Restoration of coastal grassland by means of simply reintroducing grazing, with or without initial cutting back of reed, but certainly without any application of intensive and destructive methods for reed reduction (e.g. top soil removal or herbicide application), does not succeed in changing the soil properties for at least the first 5 yr following restoration. This does not imply that such restorations are unsuccessful; as our results demonstrate, the vegetation of restored sites has reverted to a relatively similar state to traditionally managed (grazed) sites in terms of most properties. Thus, there is a considerable decrease in addition of organic matter to soil and the impact that plant litter (through both quantity and quality) has on soil formation has reverted to a state similar to managed (i.e. desired state) coastal meadows. Moreover, even though the soil N content and C/N ratio of restored sites is still similar to that of abandoned sites, the plant N content of restored sites is already similar to that of the managed sites, which indicates increased availability of N for plants and, hence, increased N mineralization in soil. If management of these areas continues, and new input of nutrients into the system can be avoided, the restoration of typical coastal grasslands should be possible. However, changes in soils take much longer than changes in above-ground properties of the plant community (see also Onaindia et al. 2001; Klimkowska et al. 2007; Van Dijk et al. 2007). This discrepancy should be considered when planning the duration of restoration projects as well as monitoring of restoration success.

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The DCA axes show that species composition of the studied communities is primarily related to management regime and lushness of the vegetation. Obviously, these two aspects are negatively correlated, as grazing efficiently disturbs the vegetation and reduces the level of dominance by tall species. The second DCA axis is more complex and demonstrates the transition from species-rich pH-neutral (or even slightly alkaline) communities to moist, C- and organic matter-rich (peaty) communities. Ordination very clearly highlights the large variation in coastal communities (as also emphasized by differences between study regions in both vegetation and soil properties), especially variation in vegetation of abandoned sites. Not all reedbeds are species-poor; Vestergaard (1998) decribes multi-species *Phragmites*-dominated communities in the geolittoral of Danish coasts. In our study areas, reedbeds have more species if they are on drier or shallower soils (negative end of the second DCA axis) or have not yet fully developed. In such cases, the dominance of *Phragmites* is not as strong and several other competitive species with high growth rates dominate (e.g. *Elymus repens*, *Filipendula ulmaria*, *Lythrum salicaria* and *Angelica sylvestris*). The latter sites can be initially quite species-rich (see also Jutila 1997; Wanner 2009), but it is not certain whether their diversity can persist when the reedbed continues to develop. High small-scale species density (number of species per unit area) is not typical for coastal meadows and the richness of plant species alone is not usually the goal of conservation. In Estonia, these habitats are restored for protection of low-stature vegetation, suitable for small plants and specific groups of birds and amphibians. Surprisingly, even though the vegetation of restored sites seemed very different from the vegetation of continuously managed sites during the site selection process, and the distinction between these two groups in the DCA ordination is fairly clear, the typical coastal grassland species were relatively common (in terms of occurrence) in restored areas (Fig. 3). Thus, just 5 yr of restoration has been sufficient for developing early similarities in vegetation of restored and continuously managed coastal grasslands. We must point out, however, that this early success is fragile. First, the relatively common occurrence of typical coastal grassland species does not imply that they are also abundant. Second, *Phragmites australis* is still present in 52% of relevés of the restored sites (Appendix S1), and when present covers on average 10% of the relevé. Thus, whenever there is a drop in the grazing intensity, *Phragmites* and other highly competitive species that are still commonly present (e.g. *Deschampsia cespitosa* and *Filipendula ulmaria*) will flourish and the small species may be rapidly out-competed (pers. obs., see also Bakker 1989; Bakker et al. 1997). Therefore, it is essential to maintain efficient management of restored sites when evaluating the success of restoration, and to pay attention not only to the presence of favourable target species but also to the presence of species that are responsible for degradation of the habitat and the factors that benefit abundance of unfavourable species, such as accumulation of biomass and nutrients in soil.

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Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1. Relative occurrence of species in relevés of differently managed sites. Species with relative occurrence value at least 0.05 in at least one of the management groups are presented in the table. Species are ordered in a decreasing order of occurrence. Number of relevés per each group: managed sites – 120; restored sites – 60; abandoned sites – 100. *Denotes species which could be used as indicators of restoration success (typical species of Boreal Baltic coastal grasslands).

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